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Changes in Structure and Composition of a New Zealand Lowland Forest Inhabited by Brushtail Possums[1]

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ABSTRACT: All specimens of 19 tree and 11 shrub species greater than 10 cm dbh (more than 3000 stems of trees and tree ferns) were labeled, measured, and mapped in 2.25 ha of lowland forest near Wellington, New Zealand. Their fate, growth, and additional recruitment were monitored in three surveys over 16 yr, from 1969 to 1985. During the vegetation study, movements, diet, density, and breeding success of the introduced Australian brushtail possum (*Trichosurus vulpecula*) were studied in the same area of forest. In the study plot the number of stems and their total basal area increased between 1969 and 1985. However, several species that are eaten by possums have suffered substantial losses of both stems and total basal area. These include *Beilschmiedia tawa*, *Weinmannia racemosa*, *Metrosideros robusta*, and the tree fern *Cyathea medullaris*. Species not eaten by possums have increased in both numbers and basal area. These include *Hedycarya arborea*, *Cyathea smithii*, *Cyathea dealbata*, and *Laurelia novae-zelandiae*. During the study there has been a decline in basal area of emergent trees, an increase in basal area of canopy trees (but little increase in their numbers), and an increase in numbers and basal area of minor species and dead trees. If present trends in structure and composition of this lowland forest continue, the future forest will have a greater proportion of tree ferns and more short-lived, small-diameter species. Canopy height and species diversity are also likely to decrease.

POSSUMS (*Trichosurus vulpecula*) were introduced to New Zealand from Australia during the 1850s and thereafter were liberated extensively to establish a fur industry. They are herbivorous and have adapted to eating a wide range of plants in New Zealand, although clearly feeding on some plant species more than others (Pracy and Kean 1949, Kean and Pracy 1953, Mason 1958, Kean 1959, Fitzgerald 1976). Continued browsing defoliates and ultimately kills many of their food trees (Meads 1976, Fitzgerald 1978, Batcheler 1983), with serious consequences for the composition and structure of native forests.

Possums were introduced to catchments adjacent to the Orongorongo Valley, near Wellington, in 1893 and 1894 (Pracy 1962). If they spread from these catchments at a rate similar to that of possums in the Fox catchment in the South Island (0.8–1.6 km/yr [Pekelharing and Reynolds 1983]), they could have become numerous in the Orongorongo Valley between 1920 and 1930. Possums were completely protected in the Wellington Acclimatization District up to 1916 so that their numbers could build up, but from 1921 they were sufficiently common in the Orongorongo Valley for the New Zealand Forest Service to trap them. In 1946–1947, after possum numbers peaked, 1024 possums were killed in just 1 yr from a strip of about 230 acres (93 ha) (Mason 1958). Part of that strip is now included in a Department of Scientific and Industrial Research (DSIR) area for research into forest ecology (Campbell 1984). The density of possums is still about 9–12/ha (Brockie 1982) and has apparently changed little since the early 1940s (M. G. Efford, pers.

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comm.). Numbers seem to be largely unaffected by drastic changes in the food supply brought about by the loss of palatable plants, but the mean weights and breeding productivity of the possums seem to have declined since the 1950s (Bell 1981).

Study Area

The Orongorongo River is one of the main southward-flowing rivers in the Rimutaka Range, east of Wellington (Figure 1). Ecology Division, DSIR, has a field station about 12 km upsteam on the east bank of the river at 130 m altitude. It is situated in a clearing in lowland forest growing on Pleistocene fan gravels (Campbell 1984). The forest consists of emergent *Metrosideros robusta* and *Dacrydium cupressinum* over a very uneven upper canopy of tall *Laurelia novae-zelandiae* and *Knightia excelsa*, which in turn are often emergent over a lower canopy of *Elaeocarpus dentatus*, *Melicytus ramiflorus*, *Hedycarya arborea*, and tree ferns (Figure 2). In this forest *Metrosideros robusta* establishes as an epiphyte high in the crowns of other trees and sends down roots that clasp the host tree. When the host tree dies, *M. robusta* remains as a free-standing emergent tree. In contrast to many terrestrial stands of *Metrosideros*, these epiphytic trees do not establish synchronously.

Over the years the understory of the forest has been browsed intermittently by goats (*Capra hircus*), deer (*Cervus elaphus*), and straying cattle (*Bos taurus*). Canopy trees have been browsed by possums. Since 1965 populations of introduced animals within the DSIR study area have been left to reach their natural limits. Because possum numbers were high throughout the Orongorongo Valley, a control study area with no possums was not feasible.

The climate is mild and moist, with a mean summer temperature of 15.9°C, mean winter temperature of 7.5°C, and average annual rainfall of about 2500 mm, with a winter maximum. Rainfall is generally reliable, but there are sometimes "droughts" with less than two-thirds of the mean monthly fall for 5–7 months (Campbell 1984). Rare cyclones of tropical origin bring high winds and heavy rainfall. A violent storm in early 1936 blew down trees near the present study area.

Brushtail Possum Biology

In the study area, most possums, if they survive their first year, live on average for a further 5 yr, and some until they are 10 or 12 yr old (Crawley 1970, Brockie et al. 1981). Possums generally have stable but not exclusive home ranges (Gilmore 1967, Crawley 1973, Jolly 1973, Ward 1978), and centers of activity usually change slightly from season to season and from year to year (Ward 1978). They may move outside their normal range to feed on seasonally occurring foods regardless of whether resident animals are already there.

Possum diet in the Orongorongo Valley is well known, both currently and historically. *Metrosideros robusta* and *Weinmannia racemosa* together at present contribute 60% of the leaves eaten by possums on the study plot (Fitzgerald 1976, 1978) and have been part of the diet of possums there since the 1940s (Mason 1958). Possums today still depend largely on the same species that formed the bulk of their diet in the 1940s, although some species eaten then do not feature now because they are no longer available (Fitzgerald 1976, 1978, Campbell 1984). Over a wide area of the forests in the Orongorongo Valley, many of the early pioneer or later seral species (such as *Alectryon excelsus*, *Plagianthus regius*, *Myrsine salicina*, *Fuchsia excorticata*, *Pseudopanax arboreus*, *Aristotelia serrata*, and *Coriaria arborea*) are now rare or absent, largely because possums have killed the adult trees and goats and deer the seedlings (Campbell 1984). During the present study, no seedlings of *Fuchsia excorticata*, *Pseudopanax arboreus*, *Aristotelia serrata*, and *Plagianthus regius* were found in any light gaps, although adult trees were present in the 1940s to 1950s (Mason 1958; L. T. Pracy, pers. comm.). In 1946–1947 possums apparently did not eat *Beilschmiedia tawa* leaves (Mason 1958). However, 25 yr later leaves of this tree were a regular dietary item (Fitzgerald 1976).

Possums eat the foliage of trees and vines and also the flowers, flower buds, and fruit of

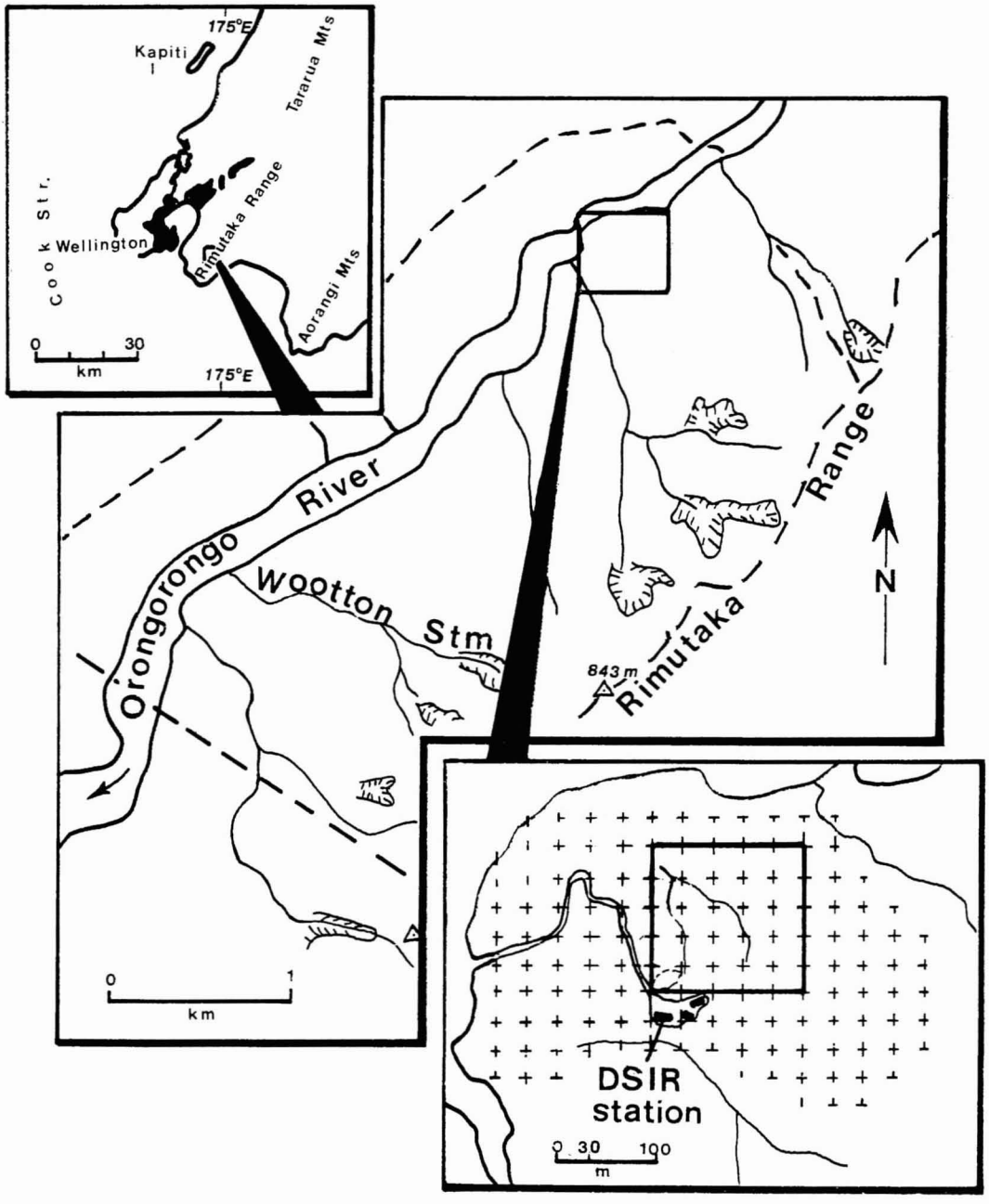

FIGURE 1. Location of the study area.

FIGURE 2. View of the forest canopy, from a 30-m tree platform, near the center of the study area.

many species (Kean and Pracy 1953), reducing the potential seed crop for regeneration and the amount available for birds. When possum numbers are reduced, the flower buds and flowers of species such as *Rhopalostylis sapida* and *Elaeocarpus dentatus* remain and the trees fruit prolifically (P. E. Cowan, pers. comm.).

The lowland forest of the Orongorongo Valley supports a far greater biomass of mammals (mainly possums) than comparable forests elsewhere in the world (Brockie and Moeed 1986). The additional browsing pressure from possums and the type of browsing pressure they impose, together with the characteristics of the trees themselves (such as long-lived leaves and an inability to produce new foliage when browsed), have made some tree species particularly vulnerable and brought about much of the change in the forest.

Captive possums maintain body weight by eating 400–500 g fresh weight of leaves daily (Fitzgerald 1981), and free-living adult animals weighing 2.3 kg (the average body weight in the Orongorongo Valley) require at least 300 g daily (P. C. Cowan, pers. comm.). In that area, the diet of possums includes on average 29% *Metrosideros robusta* leaves and 33% of *Weinmannia racemosa* (Fitzgerald 1976). Assuming that every possum eats 300 g per night, at least 640 leaves of *M. robusta* and 290 of *W. racemosa* are eaten per possum per night. On average, 23 ± 3 possums use the 2.25-ha study area, and during the year these animals eat $5.4 \pm 0.7 \times 10^6$ leaves of *M. robusta* and $2.4 \pm 0.3 \times 10^6$ *Weinmannia* leaves.

Possums usually eat old leaves, and the trees are not stimulated into producing fresh shoots (Meads 1976, Fitzgerald 1978). As many as four animals may feed at once in the same tree (Meads 1976). Older trees are more susceptible to loss of foliage than young ones (Payton 1983, 1985; Leutert 1988), and heavy browsing of *Metrosideros robusta* for three to five successive years is sufficient to kill a tree (Meads 1976). Between 1969 and 1974 fifty epiphytic *M. robusta* were assessed monthly for possum browsing (Meads 1976). By 1974

FIGURE 3. Tree of *Metrosideros robusta* defoliated by possums, with leaves remaining only on a few inaccessible twigs. Trees such as this recover if possums are excluded.

eleven of these trees were dead and all that died had been severely browsed by possums for several years. *Metrosideros robusta* trees that have no foliage except for a few tuffs on inaccessible branch tips (Figure 3) recover if possums are excluded from them (Meads 1976). Thus possums are the primary cause of death of these trees and not lack of vigor or other environmental factors.

Trees of *Metrosideros robusta* in the Orongorongo Valley have been dying since the 1930s (R. I. Kean in Campbell 1984). Aerial photographs taken in 1941 showed a few recently dead *M. robusta* trees, whereas photographs taken in 1968 showed many recently dead trees and stagheads (dead trees that have lost all but the main branches). Throughout the Rimutaka Range trees of *M. robusta* continue to die as a result of possum browsing, and *M. robusta* is no longer found in the Aorangi Range to the east (Druce 1971). In the Ruahine Range (200 km to the north), dead trees of *M. robusta* and *Weinmannia racemosa* defoliated by possums were common within 30 yr of possums first being liberated there (Elder 1965, Batcheler 1983).

Studies in mountainous catchments in the South Island have shown that stands of terrestrial *Metrosideros umbellata* and *W. racemosa* are dying and that possums are usually the primary cause of their death (Kean and Pracy 1953, Holloway 1959, Batcheler 1983, Pekelharing and Reynolds 1983, Leutert 1988). However, Stewart and Veblen (1982, 1983) and Veblen and Stewart (1980, 1982) have questioned the importance of possums as the cause of widespread deaths of *M. robusta* and *W. racemosa* trees. They postulate that synchronized stand senescence is a major reason for the widespread death of these species, and that possums have only hastened natural mortality in even-aged stands.

There are few detailed studies of the effects of possums on the forest itself, and most have been concerned with forest dominated by *Metrosideros* and *Weinmannia*. The problems of observing the effects of possums on mixed-species forest were noted by Kean and Pracy

(1953): "... [The possum's] effect upon indigenous forest has for many years continued to be the subject of sharp controversy, at least in part due to imperfect observation, for damage occurs predominantly in the higher forest strata and so is not readily observable from ground level. Further, effects are marked by the animal's strong preferences for definite species which may result in the local extermination of favoured plants in a forest that remains normal at first sight although hidden changes may have far-reaching consequences."

The purpose of this study was to describe some of these "hidden" changes in the structure and composition of a lowland forest where possum numbers, diet, and movements were also being studied intensively. In particular changes in the numbers and basal area of possum food trees in relation to other trees were measured; and the size classes that died, the species that were recruited, and the rate of change of vegetation composition and structure recorded.

MATERIALS AND METHODS

A 4.4-ha grid, marked with steel pegs spaced at 30 m, was used for a live-trapping study of possums (Crawley 1973). The central 2.25 ha of this forest was chosen for detailed vegetation studies. Within this 2.25-ha area in late 1969, all living or standing-dead trees and tree ferns with stems more than 10 cm diameter at breast height (dbh) were labeled with numbered tags fixed about 1.35 m above the ground. The lower size limit of 10 cm dbh was chosen so that the study concentrated on the adult trees and the effects of possums on them, rather than on the dynamics of juvenile and understory plants. Trees were identified to species and their girths measured, to the nearest centimeter, immediately above the tag. Coded notes were made on whether the measurement included any attached vines, or whether the tree was dead but still standing, dying, or defoliated, and whether the measurement was reliable for growth rate or basal area studies. The number of individual trees (as compared with the total number of stems) was also determined for each survey from these notes. If a tag could not be found, a check was made to determine whether the tree had died between surveys. Several species of trees were commonly multi-stemmed and branched below 1.35 m height. Each stem with a dbh greater than 10 cm was tagged and measured, and the tree was coded as multi-stemmed. The exact location of all trees with dbh greater than 30 cm was plotted with reference to the nearest grid peg, using a compass and tape measure; smaller trees with diameters of 10–30 cm dbh were recorded in the appropriate 30-m square.

In 1978 and 1985 each tagged tree was relocated, or its fate determined wherever possible, and survivors were remeasured. All untagged trees that had reached the lower size threshold of 10 cm dbh were labeled, identified, and mapped as before.

Because some of the smallest stems in each survey had not been tagged and measured, a lower size limit of 35 cm girth ($= 11.1$ cm dbh) was chosen to avoid bias during analysis. This 11.1 cm dbh lower size limit was used for all analyses and for all surveys.

The corner 30 × 30 m square in the study plot included an artificially maintained clearing in its center (Figure 1), and because both the number of stems and the total basal area (area of tree trunks at 1.35-m height) of trees in this square were more than two standard deviations outside the mean of all other squares, this square was excluded from all analyses. The area for all further analyses was thus 2.16 ha. In most of the analyses the individual units were stems rather than separate trees. With multi-stemmed trees, as many as seven stems may die if the tree dies, but conversely often a single stem may die and the rest of the tree remains alive.

RESULTS

The plot contained 30 species (Table 1). The structural categories used to divide the data in Table 1 (emergent, canopy, etc.) were based on the potential height of a species rather than its present status. On the study plot about 40% of the stems were ferns, 40% were lower

TABLE 1

NUMBERS OF STEMS AND BASAL AREA PER SPECIES FOR EACH SURVEY IN THE 2.16-HA STUDY AREA

LAYER	SPECIES	COMMON NAME	NO. OF STEMS			AGGREGATE BASAL AREA (m^2)		
			1969	1978	1985	1969	1978	1985
Emergent	*Dacrydium cupressinum* Lamb.	Rimu	4	3	3	4.39	3.72	3.73
	Metrosideros robusta Cunn.	Northern rata	28	18	17	44.90	36.06	39.85
Tall canopy	*Knightia excelsa* R. Br.	Rewarewa	39	36	37	5.84	6.40	6.59
	Laurelia novae-zelandiae A. Cunn.	Pukatea	73	79	85	27.82	33.51	31.49
	Prumnopitys ferruginea (D. Don) Lauben	Miro	6	5	4	2.58	2.20	1.46
	Prumnopitys taxifolia (D. Don) Lauben	Matai	2	2	2	4.28	4.20	4.11
Lower canopy	*Beilschmiedia tawa* (Cunn.) Kirk	Tawa	26	17	8	1.03	0.73	0.34
	Elaeocarpus dentatus (Forst. et Forst. f.) Vahl	Hinau	79	83	89	29.73	33.84	31.92
	Hedycarya arborea Forst. et Forst. f.	Pigeonwood	477	540	567	15.05	17.49	18.68
	Melicytus ramiflorus Forst et Forst. f.	Mahoe	276	300	307	12.46	14.72	14.06
	Olearia rani (Cunn.) Druce	Heketara	17	17	14	0.48	0.55	0.48
	Pennantia corymbosa Forst. et Forst. f.	Kaikomako	9	12	15	0.12	0.17	0.23
	Rhopalostylis sapida Wendl. et Drude	Nikau	15	16	16	0.52	0.55	0.60
	Weinmannia racemosa Linn. f.	Kamahi	25	9	7	2.13	1.30	1.08
Tree ferns	*Cyathea cunninghamii* Hook. f.	Cunningham's tree fern	101	123	112	3.21	3.79	3.53
	Cyathea dealbata (Forst. f.) Swartz	Ponga	244	296	304	10.34	12.64	12.33
	Cyathea medullaris (Forst. f.) Swartz	Mamaku	24	16	13	1.37	0.85	0.74
	Cyathea smithii Hook. f.	Smith's tree fern	420	509	478	8.23	10.40	10.59
	Dicksonia squarrosa (Forst. f.) Swartz	Weki	192	237	183	3.11	3.79	3.26
Seral/Understory	*Pseudowintera axillaris* (Forst. et Forst. f.) Dandy	Horopito	92	100	95	1.27	1.41	1.41
	Schefflera digitata Forst. et Forst. f.	Pate	80	106	100	1.72	1.90	1.79
Minor trees and shrubs	*Carpodetus serratus* Forst. et Forst. f.	Putaputaweta	4	5	9	0.07	0.11	0.20
	Coprosma areolata Cheesem.		3	3	1	0.04	0.04	0.01
	Coprosma grandifolia Hook. f.	Kanono	1	—	1	0.01	—	0.02
	Coprosma robusta Raoul	Karamu	—	2	2	—	0.03	0.03
	Corynocarpus laevigata Forst. et Forst. f.	Karaka	1	1	1	0.05	0.06	0.07
	Geniostoma rupestre Forst. et Forst. f. var. *ligustrifolium* (Cunn.) Conn.	Hangehange	—	2	12	—	0.02	0.18
	Myrsine australis (A. Rich.) Allan	Mapou	5	4	3	0.10	0.09	0.07
	Myrsine salicina Hook. f.	Toro	3	1	1	0.06	0.03	0.03
	Pittosporum eugenioides A. Cunn.	Tarata	1	2	3	0.09	0.11	0.15
			2,247	2,544	2,547	181.00	190.71	189.04
	Standing dead stems		178	195	228	13.70	20.31	20.34
			2,425	2,739	2,775	194.70	211.02	209.38

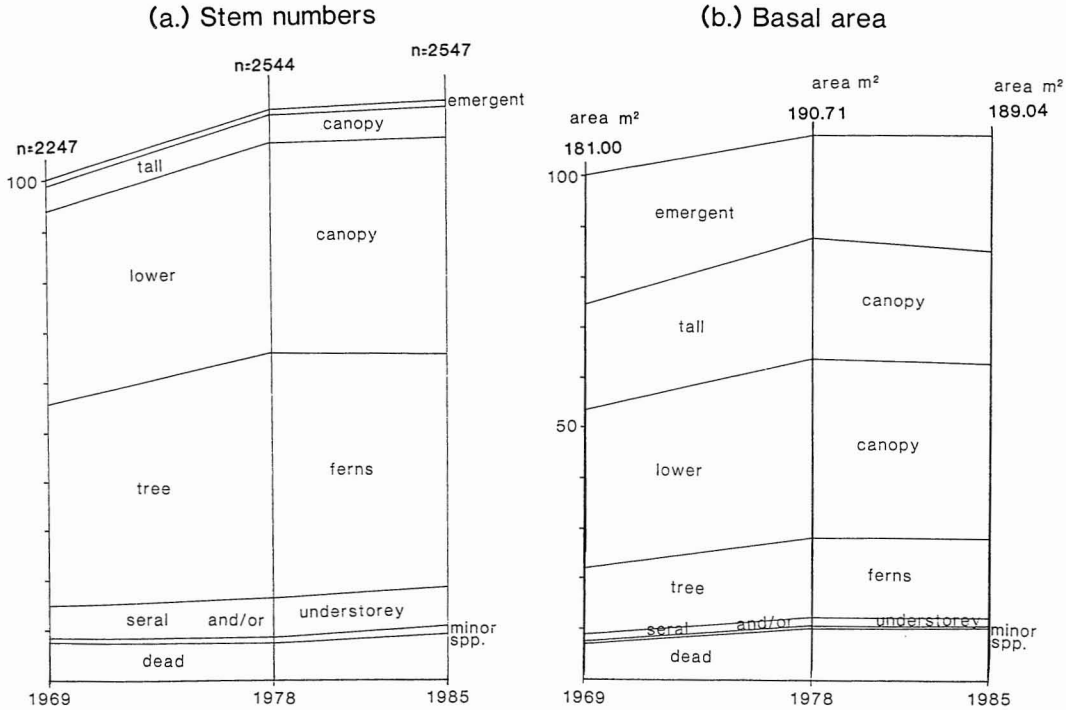

FIGURE 4. Changes from 1969 to 1978 and to 1985 in (*a*) stem numbers, and (*b*) basal area. Trees are grouped, as in Table 1, according to potential structural position in the forest. Stem numbers or basal area in 1969 shown in the left-hand column have been scaled to 1969 = 100, and the length of the intercepts for stem numbers or basal area in 1978 and 1985 are proportional to the 1969 figures.

canopy species, and the remaining 20% were 18 other species combined (Figure 4*a*).

Although there were few emergent trees (Figure 4*a*), they represented about 30% of the basal area of the forest (Figure 4*b*). The tall canopy contributed about 20% of the total basal area, and, although numerous, the tree ferns made up only about 10% of the total basal area. The seral/understory and minor species together contributed only a small fraction of the total basal area (Figure 4*b*). Species were divided into two groups: major species were those with 10 or more stems in the 2.16-ha study area, or a basal area of at least 0.2 m^2; minor species were those with fewer than 10 stems, or a total basal area of less than 0.2 m^2 (Table 1). The plot contained 21 major and 9 minor species.

The lower canopy stratum contributed most to the basal area of the forest (Figure 4*b*), and there were almost as many stems of lower canopy trees as of tree ferns. The change in total basal area in the lower canopy species is shown in Figure 5*b*. Lower canopy tree numbers (Table 1) are shown separately in Figure 5*a*. Stems of *Melicytus ramiflorus* and *Hedycarya arborea* both increased between 1969 and 1978 and again between 1978 and 1985. The number of *Elaeocarpus dentatus* stems changed little between 1969 and 1985, but *Beilschmiedia tawa* and *Weinmannia racemosa* both had fewer stems in 1985 than in 1969. The number of stems of the 10 minor species, together with *Olearia rani*, *Pennantia corymbosa*, and *Rhopalostylis sapida* did not change, and their basal area remained virtually constant. The basal area of *Hedycarya arborea* increased between 1969 and 1985, whereas those of *Melicytus ramiflorus* and *Elaeocarpus dentatus* increased between 1969 and 1978 but then decreased so that their basal areas in 1985 were only slightly greater

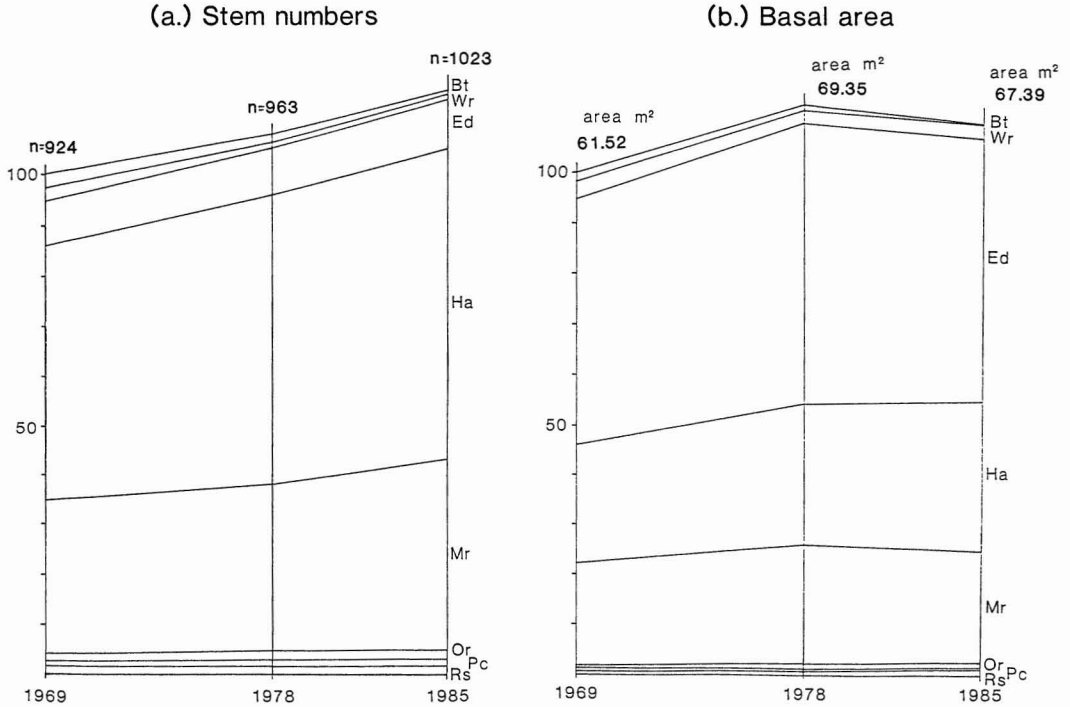

FIGURE 5. Changes from 1969 to 1978 and to 1985 in (*a*) stem numbers, and (*b*) basal area of trees growing in the lower canopy (see also caption to Figure 4). Bt = *Beilschmiedia tawa*, Ed = *Elaeocarpus dentatus*, Ha = *Hedycarya arborea*, Mr = *Melicytus ramiflorus*, Or = *Olearia rani*, Pc = *Pennantia corymbosa*, Rs = *Rhopalostylis sapida*, Wr = *Weinmannia racemosa*.

than in 1969. The basal area of both *Weinmannia racemosa* and *Beilschmiedia tawa* decreased steadily from 1969 to 1985.

Stem Numbers

The survival to 1985 of single-stem trees alive in 1969 is shown in Figure 6. These stems were of mixed age when measured in 1969, and their survival depended partly on the age of each tree relative to the average longevity of the species. The survival from 1969 to 1985 of long-lived trees such as *Laurelia novae-zelandiae* (97%) and *Elaeocarpus dentatus* (96%) contrasted with that of short-lived species such as *Schefflera digitata* (54%) and *Pseudowintera axillaris* (66%), which were usually near the end of their life span by the time they reached the lower size limit of 10 cm dbh. Although both *Beilschmiedia tawa* and *Weinmannia racemosa* are long-lived trees, their survival rates in this forest are below those of *Shefflera digitata* and *Pseudowintera axillaris*.

To understand the changes in stem numbers (and basal area), data for stem recruitment and mortality were separated from those for growth of existing stems. Turnover of several species was greater than the net change in their numbers, especially (Figure 7) for species associated with the dynamics of recruitment and mortality in light gaps, such as *Hedycarya arborea*; *Melicytus ramiflorus*; *Pseudowintera axillaris*; the tree ferns *Cyathea cunninghamii*, *C. dealbata*, *C. smithii*, and *Dicksonia squarrosa*; and the minor species.

A detailed examination of the numbers of stems from 1969 to 1985 revealed the fate of stems and trees throughout the period (Table 2). No fallen trees were included in the 1969 survey, and new stems were added only during the 1978 and 1985 surveys. By 1985 *Beil-*

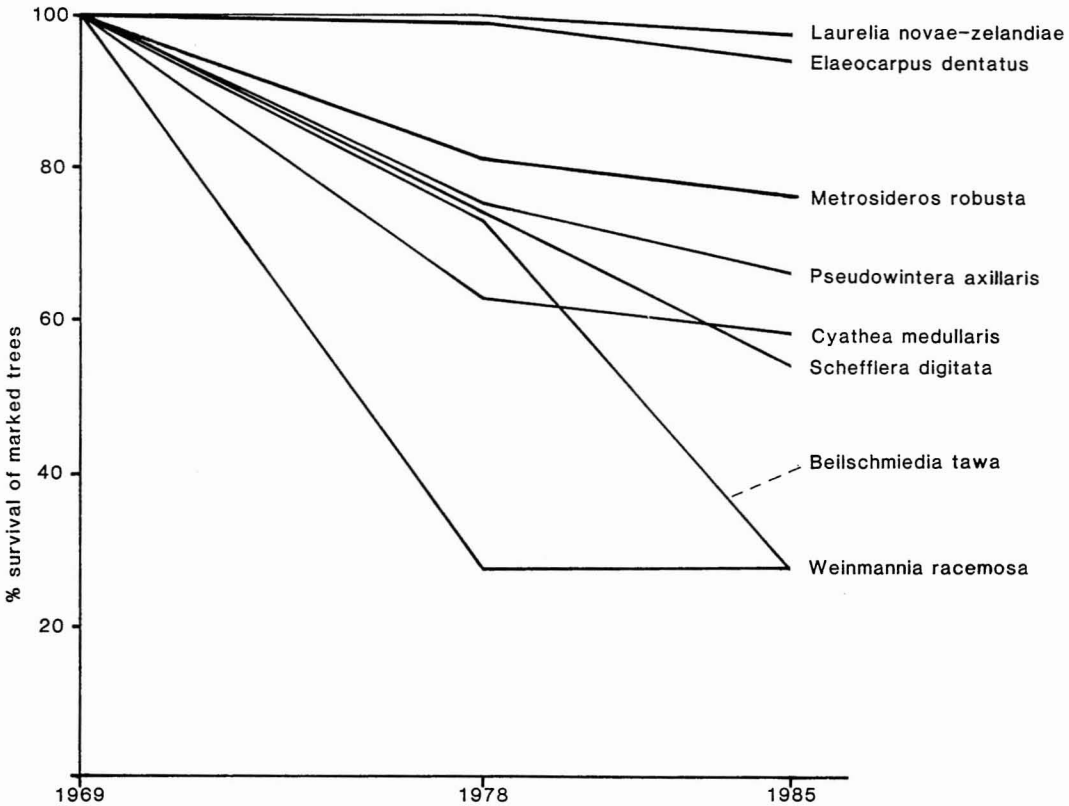

FIGURE 6. Survival of marked trees between 1969 and 1985.

schmiedia tawa had lost two-thirds of the stems and gained no new ones. Half the stems of the tree fern *Cyathea medullaris* had been lost by 1985 and no new ferns recruited except for three that established on the edges of the grassy clearing in the square excluded from analysis. By contrast, *Elaeocarpus dentatus* is a long-lived tree that is not severely browsed by possums; it had few deaths and a gradual rise in live stems. *Schefflera digitata*, a short-lived species, showed a rather different pattern of recruitment and mortality. By 1985 *S. digitata* stems had increased by half. In 1969 *Weinmannia racemosa* had 25 live stems and 8 dead; by 1985 seven were alive, 15 were dead but standing, and 4 had fallen. No new stems were added. The depressed recruitment of *Cyathea medullaris* relative to the other tree fern species is shown in the frequency histograms (Figure 8).

Frequency histograms of stem numbers of three multi-stemmed and three monopodial trees are shown in Figure 9. Although *Melicytus ramiflorus* is browsed by possums, it did not show a decline in numbers, presumably because of its ability to produce new growth, whereas both *Weinmannia racemosa* and *Beilschmiedia tawa* had fewer stems in 1978 and again in 1985. In contrast to the other species, both *Weinmannia* and *Beilschmiedia* lost small-diameter stems, and these stems did not appear in the larger size classes. Because *Metrosideros robusta* is epiphytic, meaningful "stand" data would have to be obtained from above the point of establishment on the host tree, which is often more than 20 m above ground.

Figure 10 summarizes the changes in the number of stems of individual species between 1969 and 1985, plotted on a logarithmic scale

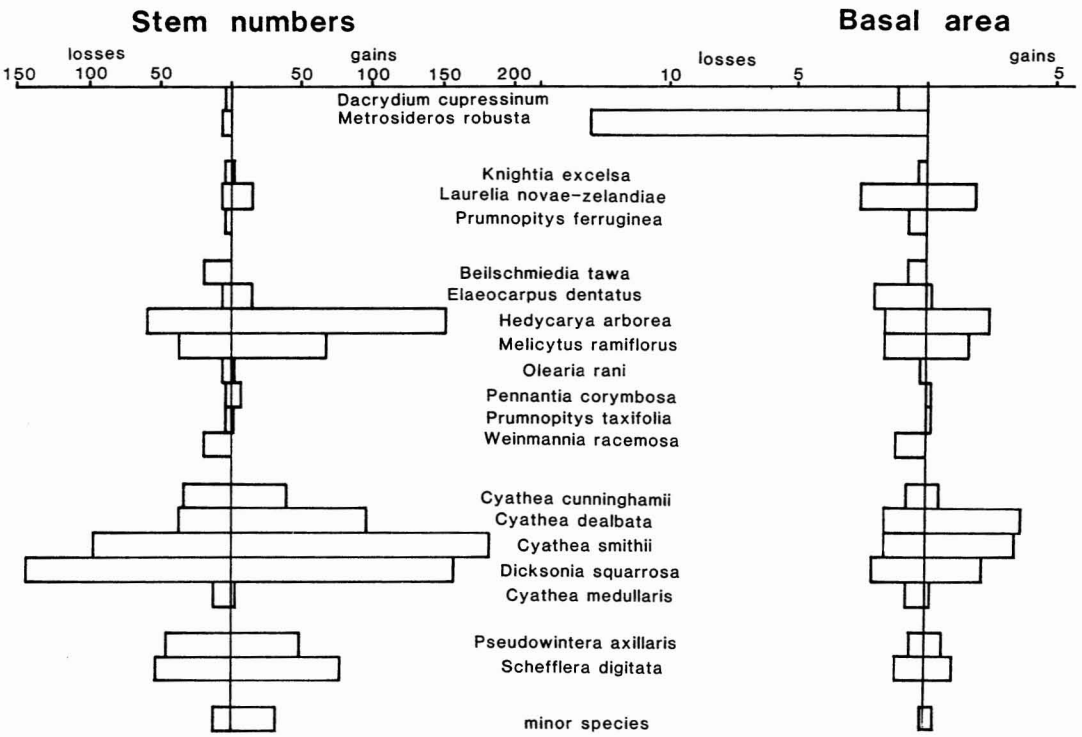

FIGURE 7. Losses and gains in stem numbers and basal area, 1969–1985. Trees are grouped according to structural layers, as in Table 1.

TABLE 2

TURNOVER OF STEMS OF FOUR TREE SPECIES AND ONE TREE FERN

	1969		1978				1985			
	STEMS		STEMS				STEMS			
SPECIES	LIVE	ds*	LIVE	ds	df†	NEW	LIVE	ds	df	NEW
Beilschmiedia tawa	26	6	17	8	11		8	12	5	
Cyathea medullaris	24	12	16	13			13	12		
Elaeocarpus dentatus	79		83	1		5	89	3	1	3
Schefflera digitata	80		56	11	13	50	105	12	1	26
Weinmannia racemosa	25	8	9	17	7		7	15	4	

*ds, dead and standing.
†df, dead and fallen.

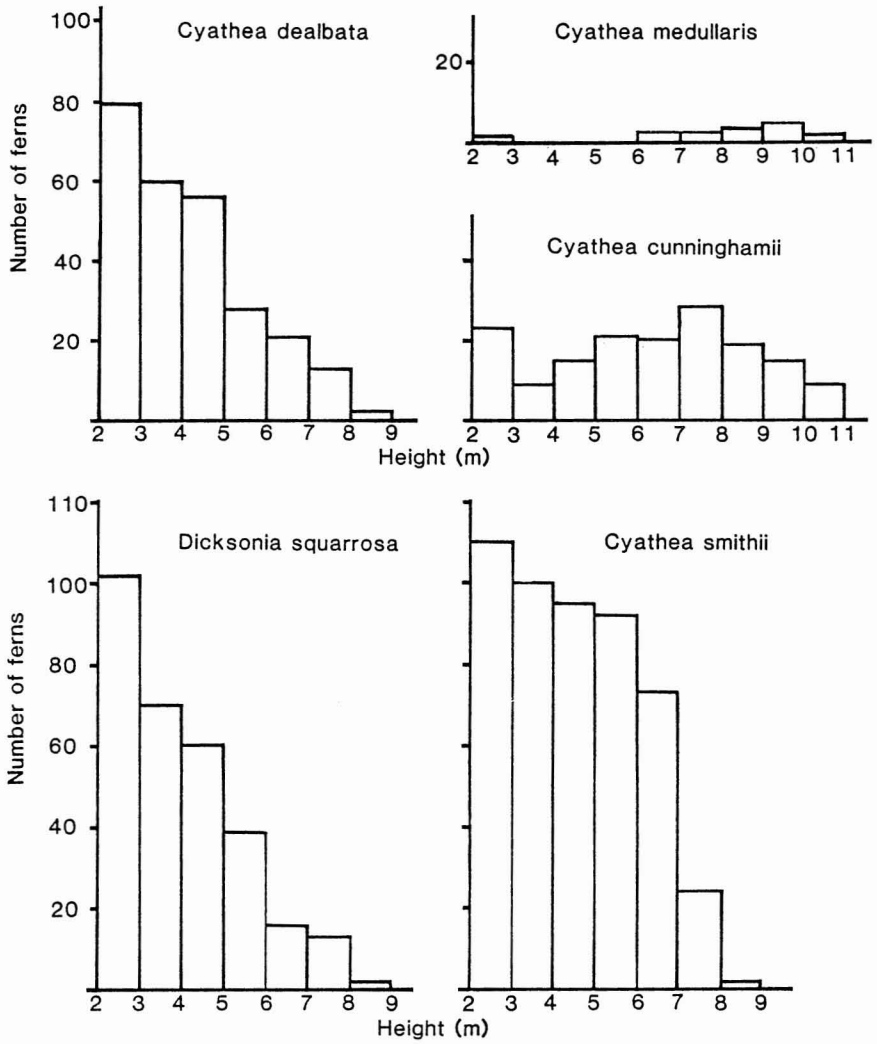

FIGURE 8. Frequency histograms of tree fern heights, 1979.

so that the direction and rate of change can be compared directly between species. A few (but a substantial proportion) of the large trees *Prumnopitys ferruginea* and *Dacrydium cupressinum* died between 1969 and 1985. There was a rapid loss of *Weinmannia racemosa* stems between 1969 and 1978, with a further slight decrease to 1985. The numbers of *Beilschmiedia tawa* stems declined steadily between 1969 and 1985. One *Metrosideros robusta* tree fell, and three others that were severely defoliated died between 1969 and 1978. By 1985 a further tree had died and another was defoliated but still alive. Both the *Weinmannia* and the *Metrosideros* trees that died were separate from others of the same species, which suggests that more possums visited them and the browsing pressure was more severe. In each of the three surveys, *Hedycarya arborea* had the greatest number of stems, and the numbers of both stems and separate *H. arborea* trees increased by 21.6% between 1969 and 1985. The numbers of the second most common species, the tree fern *Cyathea smithii*, rose between 1969

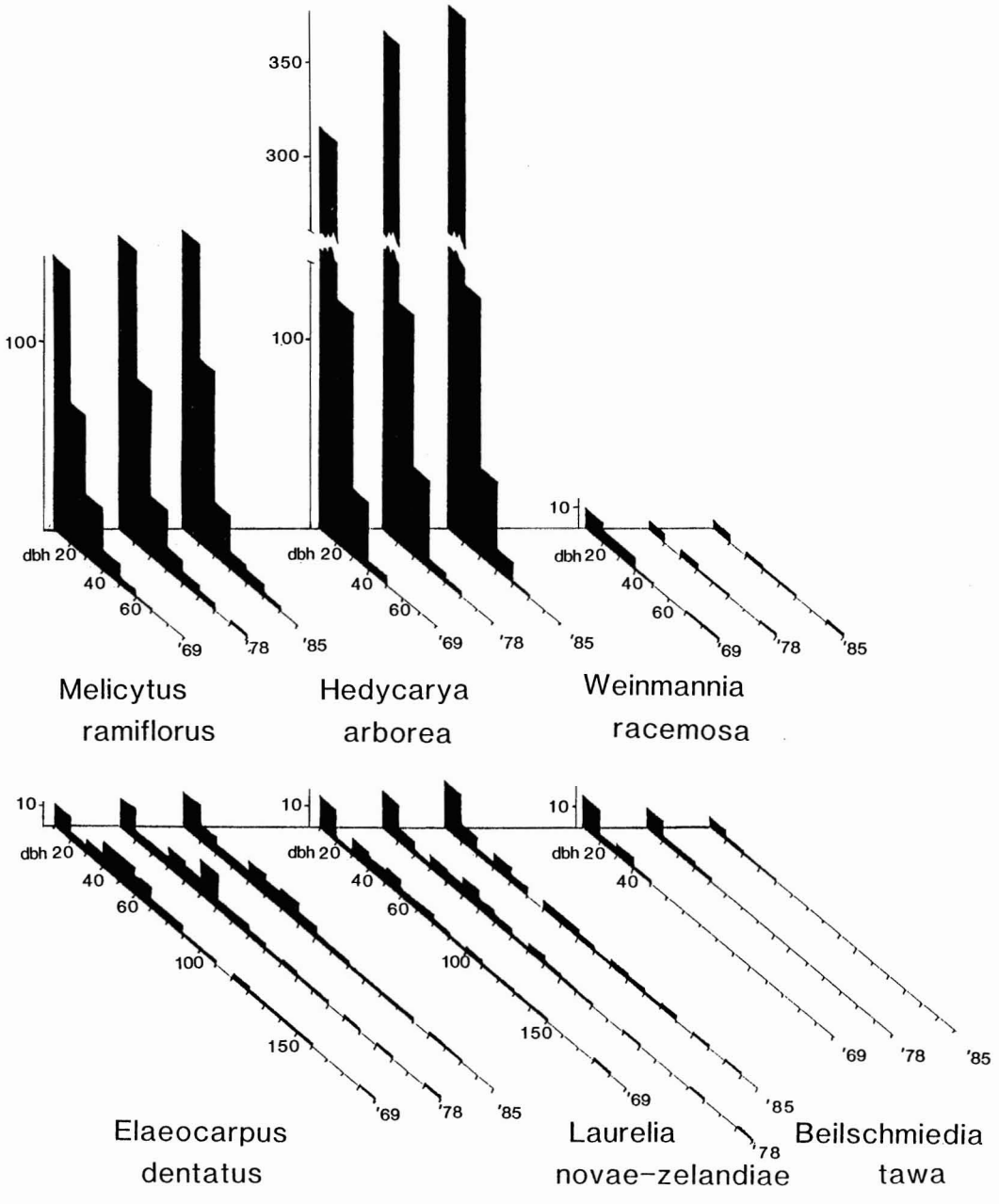

FIGURE 9. Size-class histograms of three multi-stemmed tree species (*above*), and three monopodial tree species (*below*), 1969 to 1978 and to 1985.

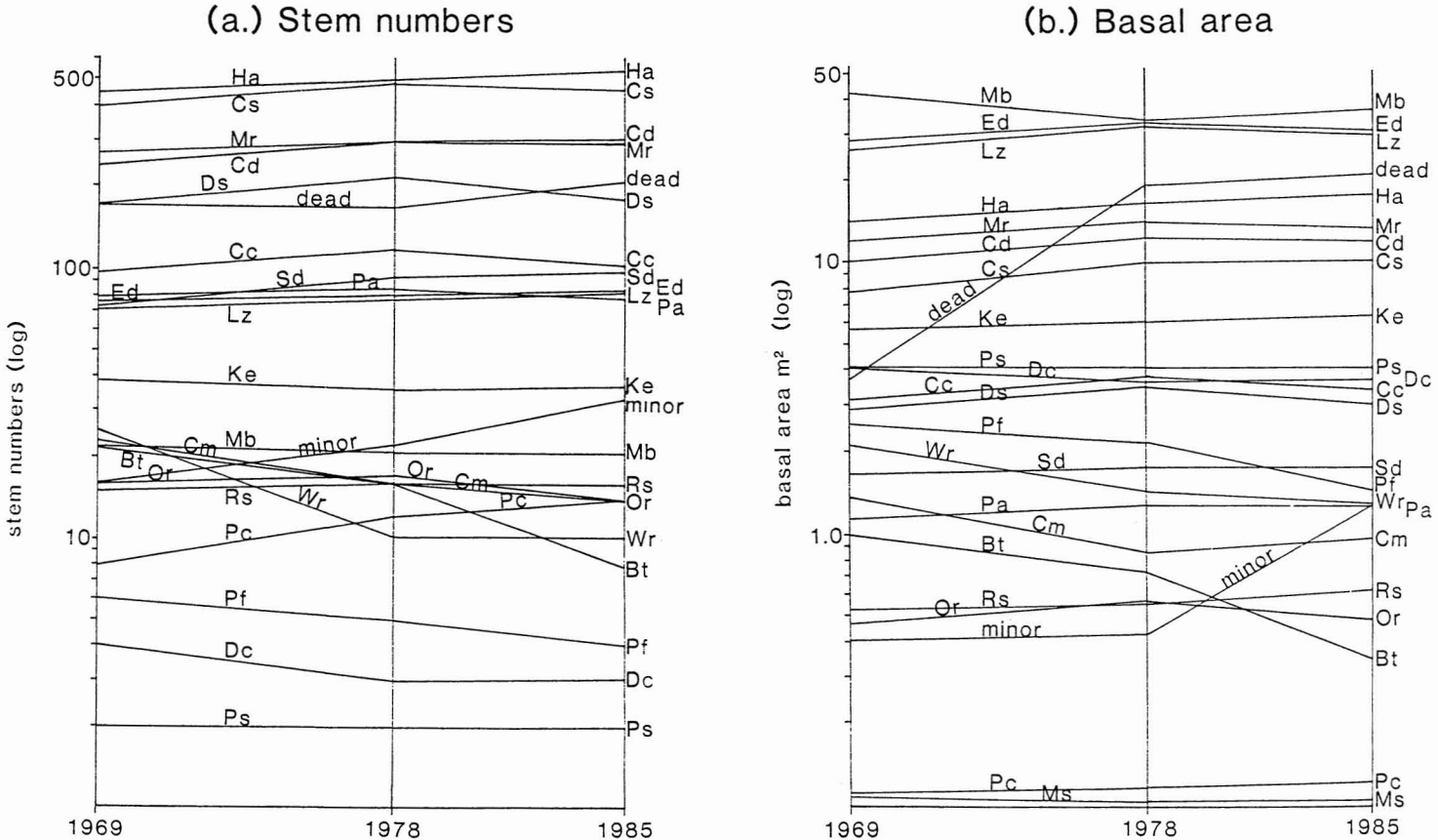

FIGURE 10. Changes from 1969 to 1985 in abundance and basal area of trees, plotted on a logarithmic scale; (*a*) changes in stem numbers, (*b*) changes in basal area. Bt = *Beilschmiedia tawa*, Cc = *Cyathea cunninghamii*, Cd = *Cyathea dealbata*, Cs = *Cyathea smithii*, Dc = *Dacrydium cupressinum*, Ds = *Dicksonia squarrosa*, Ed = *Elaeocarpus dentatus*, Ha = *Hedycarya arborea*, Ke = *Knightia excelsa*, Lz = *Laurelia novae-zelandiae*, Mb = *Metrosideros robusta*, Mr = *Melicytus ramiflorus*, Ms = *Myrsine salicina*, Or = *Olearia rani*, Pa = *Pseudowintera axillaris*, Pc = *Pennantia corymbosa*, Pf = *Prumnopitys ferruginea*, Ps = *Prumnopitys taxifolia*, Rs = *Rhopalostylis sapida*, Sd = *Schefflera digitata*, Wr = *Weinmannia racemosa*; minor species are listed in Table 1.

and 1978. Although *C. smithii* numbers declined again between 1978 and 1985, there was a 19% increase overall. Between 1969 and 1985 the numbers of stems of *Melicytus ramiflorus*, the third most common tree, increased by 10%. *Cyathea dealbata* increased 24.7% between 1969 and 1985, more between 1969 and 1978 than later. The numbers of the tree fern *Dicksonia squarrosa*, on the other hand, increased substantially between 1969 and 1978, but by 1985 many had died, leaving an overall increase of only 5.8%. The decrease in numbers of *D. squarrosa* between 1978 and 1985 was probably reflected in the 23% increase in the number of standing dead stems over the same period.

The number of *Cyathea cunninghamii* increased by 6% between 1969 and 1985, despite a decline after 1978. *Elaeocarpus dentatus* and *Laurelia novae-zelandiae*, both of which were present as large trees, had a few more stems in both 1978 and 1985. Stem numbers of *Schefflera digitata*, a tree normally associated with light gaps or forest edges, increased from 1969 to 1978 and again to 1985. *Pseudowintera axillaris* had the same number of stems over the 16 yr, but both *Pseudowintera* and *Schefflera* had a substantial turnover of individuals between surveys (Figure 7). *P. axillaris* is a small tree with distasteful peppery foliage that is not fed on by browsing animals, and because dead trees decay and disappear rapidly, the high numbers of *P. axillaris* trees in the study area probably resulted from higher numbers of hoofed animals in the area some decades before the first survey.

The other two notable changes were increases in minor species (106% increase from 1969 to 1985) and *Pennantia corymbosa* (66.6% increase, 9 stems to 15, from 1969 to 1985), again suggesting past effects of hoofed animals.

Basal Area

Figure 10*b* shows the changes in basal area from 1969 to 1985. The most dramatic change was the increase by almost 150% in the basal area of standing dead trees. This was largely because several large trees died, the number of dead standing stems did not show the same increase between 1969 and 1978, and large trees that had fallen were not measured. The six largest trees that died between 1969 and 1978 were (dbh in parentheses): *Metrosideros robusta* (219, 111, and 78.9 cm), *Dacrydium cupressinum* (120 cm), *Weinmannia racemosa* (82.4 cm), and *Elaeocarpus dentatus* (78.9 cm). Another dramatic change, although insignificant in terms of total basal area, was the marked increase in the basal area of minor species between 1978 and 1985 mainly because of increased numbers of *Schefflera digitata.*

The reduction of basal area between 1969 and 1978 of trees of *Metrosideros robusta* (the species with the greatest total basal area on the study area) did not continue to 1985, as the increments from living trees exceeded losses. The basal area of *Elaeocarpus dentatus* and *Laurelia novae-zelandiae* trees increased between 1969 and 1978, then decreased slightly between 1978 and 1985 because one large tree of each died, but ended with larger basal area than in 1969 (7% and 13%, respectively). The basal area of trees of *Hedycarya arborea* showed a steady (25%) increase from 1969 to 1985. Basal area in *Melicytus ramiflorus*, by contrast, first showed an increase between 1969 and 1978 and dropped by 1985, resulting in a 12% increase overall. This pattern was also shown by the tree ferns *Cyathea dealbata* and *C. smithii.* The basal area in *Knightia excelsa* showed little difference between the surveys in 1969 and 1985. *Dacrydium cupressinum* was a major component of the basal area of the emergent trees, but showed a 16% decline from 1969 to 1985 because of the death of one very large tree before 1978. The total basal area of the tree ferns *Dicksonia squarrosa*, *Cyathea cunninghamii*, and *C. dealbata* showed an increase from 1969 to 1978, but after that many tree ferns died. In 1985, total basal area in *D. squarrosa* was only slightly more than in 1969, but that in *C. smithii* increased by 28%. Basal area in *Prumnopitys ferruginea*, *Weinmannia racemosa*, *Cyathea medullaris*, and *Beilschmiedia tawa* all showed an overall decline from 1969 to 1985. The most rapid loss of basal area of any species was that of *B. tawa.* The basal area of *Weinmannia racemosa* also

declined sharply between 1969 and 1978, but rather less from 1978 to 1985.

DISCUSSION

Stem Numbers and Trends in Composition

Over the 16 yr from 1969 to 1985, the numbers of stems of most species changed because of the death of large trees by chance tree falls, the death of standing trees from natural causes and from possum browsing, and regeneration in the light gaps. Some of the largest trees fell during that period, and the canopy gaps were filled with lower-growing tree ferns, minor species, and short-lived seral trees. Moreover, these large trees contributed most to the basal area of the forest, and the species that replaced them did not have the potential to grow to either the same height or the same diameter. For example, one large *Elaeocarpus dentatus* that fell between 1969 and 1978 had the equivalent basal area of 23 *Dicksonia* tree ferns.

In some species, especially *Beilschmiedia tawa* and *Cyathea medullaris*, stems were lost and there was no replacement by smaller size classes. *Metrosideros robusta* and *Weinmannia racemosa* are still the main food species of possums in the study plot (Fitzgerald 1976, 1978). Although these two species lost stems between 1969 and 1978, stem numbers have remained relatively constant since. A second group of trees, where stem numbers have continued to increase despite the loss of some stems, are usually not eaten by possums or other browsing animals or are more resistant to browsing. These include *Hedycarya arborea*, *Laurelia novae-zelandiae*, *Melicytus ramiflorus*, and the tree ferns (especially *Cyathea smithii*). The increase in *Hedycarya arborea* throughout the survey suggests that it is gradually replacing species that have earlier disappeared from this forest. Differences in its survival between the surveys were not related to changes in possum numbers because possums do not browse *Hedycarya*; other factors such as a severe drought in 1970–1971 and extensive browsing of the understory by wandering cattle, particulary in 1971–1972, may also have been important. The forest was affected by deer as well as possums, thus many of the changes have resulted from the combined effects of all herbivores, rather than just possums. Structural changes that have produced light gaps have in some cases been induced by possums, but the composition of light-gap vegetation in this forest has been largely determined by browsing animals. Species that establish in the canopy gaps are those that are unpalatable to hoofed animals, and at present about half of the stems in the study area are unpalatable tree ferns (Jane and Pracy 1974).

Some old canopy gaps were clearly associated with logs, and at least some gaps date from the 1936 storm that blew down trees in the vicinity, but other patches of regeneration have no clear relationship with logs. Either the log has rotted away, or the trees died standing and decayed without trace, as often happens with *Beilschmiedia tawa* or *Alectryon excelsus*.

During the study the composition and structure of the forest plot changed toward fewer long-lived trees, more small-diameter stems, and species with rapid turnover. In the first 9 yr there was a rise in the numbers of *Hedycarya arborea*, *Melicytus ramiflorus*, and all species of tree ferns except *Cyathea medullaris*. Since then, gains in stem numbers and basal area have slowed for tree ferns but not for *Hedycarya arborea*. The decline in tree fern numbers since 1978 may represent self-thinning in light gaps. A continuing decline in numbers and replacement with other species could be expected to follow. *Dicksonia squarrosa* tree ferns are browsed by possums, but because they usually grow in dense stands and often propagate from buds on the trunks, it is difficult to separate natural from induced mortality.

Not only have possums killed adult trees in the forest and created light gaps, but many of those trees would have been seed sources for regrowth in the canopy gaps. *Pseudopanax arboreus* normally would colonize the canopy gaps, and although mature trees are found nearby, most are defoliated, and juveniles rarely reach maturity because they are browsed and die. The populations of several other plant species commonly eaten by possums are

also close to extinction in the vicinity of the study plot (Campbell 1984). One of the three remaining *Myrsine salicina* trees alive in 1969 has since been killed by possums, and the other two are defoliated. No adult trees of *Alectryon excelsus* remain on the plot or in the surrounding forest, although it was formerly a common and important tree in this lowland forest (Mason 1958) and extended up to an altitude of 400 m. A few small saplings, usually less than 1.35 m high, grew on the plot, but none were large enough to appear in the lower size class of the surveyed trees. Several mature *Beilschmiedia tawa* trees died, and defoliation by possums probably contributed to their death.

Basal Area and Structural Changes

The loss of the largest emergent trees in the forest and their replacement by smaller-diameter stems and tree ferns brings about massive changes in the forest structure through disproportionate effects on the basal area and the total biomass of the forest. The oldest and largest trees generally carry the most epiphytes, and when a tree dies a diverse habitat is lost. The numbers, and to a greater extent the basal area, of the middle-height forest trees (the larger *Elaeocarpus dentatus* and *Laurelia novae-zelandiae*) increased only slightly. However, major changes in the forest structure probably took place before the start of the study. The forest canopy is now very uneven (Figure 2). *Weinmannia racemosa* and *Beilschmiedia tawa* were probably important canopy trees, judging by the losses during this study. This uneven surface and the pattern of species associations strongly suggest that the lower parts of the present canopy (*Melicytus ramiflorus*, *Hedycarya arborea*, tree ferns, and minor species) represent old canopy gaps.

At the start of this study *Beilschmiedia tawa* was not common on the study plot, although dying and dead trees were present both in the plot and nearby. Although possums ate small amounts of *B. tawa* leaves between 1969 and 1985, and *B. tawa* trees in the study plot were defoliated, the cause of the tree mortality was uncertain. The trees died progressively from the top of the crown, and some lower branches remained in leaf for 5 to 10 yr after the upper trunk had died. Insects browsed the crowns of the *B. tawa*, and five species of geometrid moths and two species of tortricids are known to feed on *B. tawa* foliage (Knowles and Beveridge 1982). The loss of nearby trees could well have exposed the crowns of the *B. tawa* trees to frost, and thus started a slow decline in vigor subsequently hastened by possums. I. A. E. Atkinson (unpublished Botany Division DSIR report, 1985) found that when possums were common on Kapiti Island, 21 of 35 *B. tawa* trees that he was monitoring died between 1975 and 1985. The condition of the crowns of the trees was consistently worse in one catchment where possums ate more *B. tawa* leaves than in a second catchment with more mixed vegetation (A. E. Fitzgerald, pers. comm.).

Effects of Changes on Vegetation Patterns

Synchronized stand senescence is decidedly not the reason for the death of most *Metrosideros robusta* trees in lowland forest in the Orongorongo Valley. In lowland forest most *M. robusta* trees are epiphytic, and usually trees of *M. robusta* and *Weinmannia racemosa* are in mixed-aged rather than in uniform-aged stands. But between 540 and 600 m altitude in the Orongorongo Valley, fewer colonizing species are available, and several stands of *M. robusta–W. racemosa* forest formerly grew on exposed north-facing spurs. These stands of mixed *M. robusta* and *W. racemosa* were comparable to stands of *M. umbellata* in the South Islands, being of uniform age and clearly the result of synchronous establishment after windthrow. (They are similar to the stands of even-aged *Nothofagus truncata* induced by the 1936 storm on north-facing ridges at lower altitudes in the Orongorongo Valley.) The *M. robusta* and *W. racemosa* died after possums defoliated them, and the canopy is now composed of understory species that browsing animals avoid, especially *Olearia rani*, *Hedycarya arborea*, *Brachyglottis repanda*, and tree ferns. Such higher-altitude stands of *M. robusta* and *W. racemosa* could not have established if browsing animals had been present at the time of the storm,

and will only be part of the forest pattern if there are fewer introduced animals (Kean 1959). In Australia and Papua New Guinea, where arboreal marsupials are endemic, "pure" stands of food trees do not form, the forest is mixed, and food trees are scattered.

Effect of Forest Changes on the Possum Population

If the trends shown in this study continue, some of the currently favored food trees of possums will disappear from this study plot in the next 10–20 yr. By contrast, both *Hedycarya arborea* and *Laurelia novae-zelandiae*, now abundant as seedlings and small saplings, are both likely to increase in numbers and ultimately in basal area. As the larger trees from the forest are killed and eventually rot, favored den sites in the epiphyte gardens high in the emergent *M. robusta* trees are lost. Ward (1978) found that *M. robusta* was the tree most used by possums for denning by three out of the four radio-tagged possums that he was following; at Wootton Stream, where the last *M. robusta* tree died in 1971, possums often used epiphytes in the dead standing trees as den sites (P. C. Cowan, pers. comm.).

Possums affect forest composition and structure at the crudest level by reducing the numbers of particular species that are highly preferred for feeding. When these species are the major component of the forest, as in the *Weinmannia-Metrosideros* forests of the South Island, the whole forest structure collapses. Whether the numbers of possums in mixed forest will decline when these preferred food trees become scarce and widely scattered remains to be established. The high numbers of possums in most New Zealand podocarp/mixed hardwood forests suggest either that the possum diet is adjusted to the changes in forest composition, or that the degeneration of the forest has not yet reached a point where it affects possum populations.

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